LUNULATION SIMILARITIES IN THE GENUS *ARICIA* REICH. (LEP. : LYCAENIDAE) IN BRITAIN, SPAIN AND SWITZERLAND

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Introduction

THE STATUS and relationship of the Brown Argus butterfly races in Britain and other parts of Europe have caused differences in opinion for many years. Heath et al. (1984) indicated that the Brown Argus *Aricia agestis* occurs in south and central England, and the Northern Brown Argus, *Aricia artaxerxes*, in north England and Scotland. The north of England form had at one time been considered as subspecies *salmacis,* but Jarvis (1966) and Høegh-Guldberg (1966) concluded that it was merely a form of the Scottish race. The mainly univoltine colonies in North Wales, the Peak District and the Yorkshire Wolds were considered to be Northern Brown Argus.

Doubts about the status of the Peak District colonies led to comparison of their upper wing lunulation with that of bivoltine *agestis* colonies, and it was concluded that the above three univoltine areas were all *agestis* due to consistent good lunulation, while the north of England race consisted of hybrids between *agestis* and Scottish *artaxerxes*, with variable, but intermediate, lunulation. There was also interpenetration between *agestis* and *artaxerxes* (Smyllie, 1992a, 1998). Genetic tests have been in progress since 1993 and, although detailed accounts have still to be published, some information is given in the new Millennium Atlas (Asher *et al.*, 2001). This confirms that the three univoltine races mentioned above are predominantly *agestis* and that *artaxerxes* is merely a variant of the northern continental species *artaxerxes allous* (Smyllie, 1998), and not an endemic species peculiar to Scotland as some authors have maintained. The genetic jury is still out on the status of the north of England race, although a significant *artaxerxes* component is confirmed in the new Atlas, and a statement from the first researcher confirmed the presence of both *artaxerxes* and *agestis* (Janet Cameron, pers. comm., 1996). It is, however, simpler for the time being to refer to the colonies in north England and abroad as "intermediates" because of their lunulation.

During 2000, lunulation checks have been carried out on collections in Spain and Switzerland to investigate the possibility that higher altitudes in mountain areas further south correspond with poor lunulation further north, as in Scotland and Scandinavia; that lower altitudes in Spain, Switzerland and the Canaries correspond with good lunulation as in south and central England, and that sandwiched in between is a zone with variable intermediate lunulation as in north England. Data backed by statistical checks confirm that there are broad similarities. Spain contains very well lunulated, intermediate and poorly lunulated zones. Switzerland only contains intermediate and poorly lunulated zones. Possible reasons for this are discussed and a hypothesis for the history and development of the *Aricia* genus is put forward.

Material and Methods

The major source of butterflies has been museums, plus a small number of private collections. Where appropriate, data have also been collected from the field, photographs or published material (Høegh-Guldberg, 1966). The overall database contains over 4,000 specimens, and has come from 26 British museums (Smyllie, 1992a), two Spanish – The Museo Nacional de Ciencas Naturales (MNCN, Madrid) and Unidad de Zoologia de la Universidad Autónoma de Madrid (UAMZ). Two private collections also provided data, those of Dr Klaus Schurian in Germany and Herr Hans-Peter Wymann in Switzerland, while Prof. Dr Fidel Fernández-Rubio's was consulted in Madrid. All records noted the number and size of upper forewing lunules (ufl), together with the locality, as a minimum. Examination was by the naked eye. A trace and upwards counted as one lunule. Spanish *morronensis* and Swiss *allous* had very poor ufl, so upper hindwing lunules were also noted. Records were subsequently aggregated into areas or colonies. Initially, data were manipulated to provide equal numbers of males and females (Smyllie, 1992a). Later, because males proved to be less well lunulated than females, and therefore provided a more sensitive indicator of change, data were generated from males only (Smyllie, 1998). In this paper the main concern is again with male upper forewing lunules (mufl) and data are presented in tabular form. High values for 5&6 mufl% in these Tables give an indication of good lunulation. The considerable importance of "phased emergence" is discussed later, and scanning electron microscope photographs of four British eggs are commented on.

Lunulation data from Britain

Data from old English counties have been grouped together in Table 1 to give different areas, which proceed from south to north through the *agestis* zone. The statistical formula $np \pm k\sqrt{(npq)}$ is then applied in the three right-hand columns, where n is the total and p is the proportion of the total which has five or six lunules.

From Table 1 totals, $p = 661/798 = 0.828$; q is $(1-p) = 0.172$, and k is a constant = 1.96 for 5% significance. The formula gives the boundaries within which there is a greater than 95% chance of the lunulation being due to a constant factor. The limits are calculated by adding and subtracting the $k\sqrt{(npq)}$ column to or from the np one, and checking to see whether the 5&6 mufl column is inside the limits. It can be seen that all colonies are inside the limits. The same principles apply to the north of England colonies in Table 2, but here $p = 120/532 = 0.2256$, therefore $q = 1-0.2256 = 0.7744$. The consistency of *agestis* is not repeated for the north of England colonies: nos. 1-5 are all out: note that 1,2 and 5 are high, while 3 and 4 are low.

Details for Scottish colonies are given in Table 3: these will be useful in further statistical tests later.

Table 1: Lunulation data from various agestis colonies, mainly British.

No.	Locality	Total	5&6 mufl	5&6 mufl%	np	k√(npq)	*agestis?*
1	European *agestis*	50	39	78.0	41.4	5.2	Yes
2	C'wall, Devon, S'set, Dorset	88	74	84.1	72.9	6.9	"
3	Wiltshire, Glouc'shire	58	47	81.0	48.0	5.6	"
4	Hants, IoW, Sussex, Surrey	85	69	81.2	70.4	6.8	"
5	Kent	50	42	84.0	41.4	5.2	"
6	Herts.,Essex	55	48	87.3	45.5	5.5	"
7	Berks.Bucks.Oxon.B.N.R	103	87	84.5	85.3	7.5	"
8	N'fk.Suff'k.Cambs.Hunts.P.	110	92	83.6	91.1	7.8	"
9	North Wales coast	56	48	85.7	46.4	5.5	"
10	N. Wales Eyarth Rocks	27	21	77.8	22.4	3.8	"
11	Peak district	87	71	81.6	72.1	6.9	"
12	Yorkshire Wolds	17	13	76.5	14.1	3.0	"
13	Mainzer Sand	12	10	83.3	9.9	2.6	"
	Totals	798	661	82.8			

The situation in Spain

Spain contains several mountain ranges which are isolated from one another. Associated with these is the endemic *Aricia morronensis*. Although it has been said to be endangered, records from 50 localities have been gathered, in some of which it is rather abundant. It is found in all the main mountain ranges above 1000 metres. Heights at which it occurs vary from 800 to 3,000 metres and, because it is restricted to isolated habitats, the morphology from different mountain ranges is slowly diverging. There are ten different subspecies from

Table 2: Lunulation details from north of England colonies.

No.	*Locality*	Total	5&6 mufl	5&6 mufl%	np	k(√npq)	*In/Out*
1	Pickering SE88	44	18	40.9	9.93	5.43	Out
2	Perthichwareu SJ15	48	20	41.7	10.83	5.68	Out
3	Durham coast NZ44	92	6	6.5	20.76	7.86	Out
4	Durham coast NZ43	85	10	11.76	19.18	7.55	Out
5	Durham inland NZ34	29	16	55.17	6.54	4.41	Out
6	Durham inland NZ33	24	9	37.5	5.41	4.01	In
7	North Lancashire SD48	109	18	16.5	24.59	8.55	In
8	North Lancashire SD47	101	23	22.77	22.79	8.23	In
	Totals	532	120	22.56			

different localities, each with a different morphology (Munguira & Martin, 1988, 1992; Munguira et al., 1991). *Aricia cramera* occurs widely below 1000 metres over most of the Iberian peninsula, excluding the north-west tip, while *agestis* occurs less widely and mainly in the eastern half (Gómez-Bustillo et al., 1974). Distribution maps for the north of Spain (Gómez de Aizpurúa, 1977) indicate that both *cramera* and *agestis* are found frequently in the area covered, up to 130 kilometres from the north coast. The present consensus of

Table 3: Lunulation details from Scottish colonies.

No.	*Locality*	*Total*	0mufl	0mufl%	5&6 mufl	5&6 mufl%
1	North of Inverness	13	10	76.9	0	0
2	Aberdeenshire, Banff	32	16	50.0	3	9.4
3	Inverness, Nairn, Moray	39	20	42.9	2	5.1
4	Kincardine, Angus	63	35	55.6	3	4.76
5	Perthshire	117	72	61.5	2	1.71
6	Fifeshire	25	12	48.0	2	8.0
7	SE Scotland	47	15	31.9	3	6.4
8	SW Scotland	35	7	20.0	7	20.0
	Totals	371	187	50.4	22	5.93

Table 4: Male upper forewing lunules in Spanish *Aricia*

No.	Locality (Province)	CUTN	Male upper forewing lunulation (mufl)						
			0	2-4	5&6	Total	0%	2-4%	5&6%
	A. morronensis								
1	S. de Gredos (Avila)	30TUK16	13	0	0	13	100.0	0.0	0.0
2	Abejar (Soria)	30TWM12	8	1	0	9	88.9	11.1	0.0
3	All localities	-	24	1	0	25	96.0	4.0	0.0
	A. cramera								
4	Fuente Joco (Tenerife)	-	0	0	11	11	0.0	0.0	100.0
5	Segura de Toro								
	(Caceres)	29SQD27	0	0	7	7	0.0	0.0	100.0
6	Casa de Campo								
	(Madrid)	30TVK37	0	2	34	36	0.0	5.6	94.4
7	All localities	-	0	3	70	73	0.0	4.1	95.9
	A. montensis								
8	S. de Gredos (Avila)	30TUK16	1	7	4	12	8.3	58.4	33.3
9	All localities	-	3	27	10	40	7.5	67.5	25.0

opinion among Spanish lepidopterists is that *cramera* occurs all over the Iberian peninsula together with one less well lunulated subspecies which some call *montensis* and others call *agestis*. No examples of *agestis* were seen in the Madrid collections from which data was taken. Results are presented in Table 4.

The situation in Switzerland

Results are presented in Table 5. Differing opinions were summarised Gonseth (1987). Only *A. agestis* and *A. artaxerxes allous* are considered as being resident. The following aspects are mentioned: *agestis* is bivoltine and occurs below 1200m, while *allous* is univoltine and occurs above 1200m. This is complicated by reports of *agestis* at heights of 1620m in the Wallis Alps and over 1400m in the Jura, which indicates that both subspecies (so called because they can cross-breed) can fly together. There is also a report of *allous* in the lower Jura. In another paper (Bischof 1990), distribution details are given of *artaxerxes allous* in Schanfigg, Kanton Graubünden. The colonies are double-brooded between 920 and 1300m, but single brooded above 1300m. According to Gonseth (*op. cit.*), different authors disagree about whether *allous* and *agestis* belong to the same or different Taxa (Beuret, 1960; Kames, 1976; Schurian, 1994) and other aspects include occasional hybrids (Ebert & Rennwald, 1991). Gonseth therefore gives just one distribution map covering both *agestis* and *allous*. Geographical locations of the Swiss localities are given in Fig. 1.

Table 5: Male upper forewing lunules in Swiss *Aricia*

No.	Locality	Altitude	Swiss Grid	Male upper forewing lunulation (mufl)						
		müM	Reference	0	2-4	5&6	Total	0%	2-4%	5&6%
A. artaxerxes allous										
1	Val Bever (GR)	1760	785,155	12	0	0	12	100.0	0.0	0.0
2	Haldenstein (GR)	600	755,190/5	17	2	0	19	89.5	10.5	0.0
3	La Luette (WA)	950	600,110	7	3	0	10	70.0	30.0	0.0
4	Airolo (TI)	13-1800	690,150	6	7	0	13	46.2	53.8	0.0
5	Kandertal (BE)	10-1900	615,140/5	4	5	0	9	44.4	55.6	0.0
6	Mitholz (BE)	1000	615,150	6	2	0	8	75.0	25.0	0.0
7	All localities		-	61	21	0	82	74.4	25.6	0.0
	A. "agestis"									
8	Orvin (BE)	7-800	580,220	2	5	3	10	20.0	50.0	30.0
9	Chiasso (TI)	400	720,75/80	2	9	5	16	12.5	56.4	31.2
10	Crémines le Cras	720-780	600/5,235	0	5	3	8	0	62.5	37.5
11	All localities		-	4	19	11	34	11.1	58.3	30.6

Fig. 1. Swiss localities in Table 5: *allous*; + intermediates.

Statistical overview

Table 6 collects data from Britain and other parts of Europe to enable a check to be made on whether the varying numbers of males with 5&6 ufl at different sites could be due to chance. From this Table, the overall proportion of males with 5&6 ufl (p) is 925/2122 = 0.4359. It is possible to check statistically using $np \pm k\sqrt{(npq)}$ to determine if these figures are within the 5% significance limits, using the format in Table 1. Data from Scottish *artaxerxes,* north of England intermediates, and central/south England *agestis* are used because of the large data bank, and results are given in Table 7. It can be seen that none of the three British zones is within the limits necessary for the variation to be considered only a matter of chance. Spanish *morronensis* and Swiss *allous* both have no 5&6 mufl, while Spanish *cramera* is better lunulated than *agestis*, so these races will be further out than the British ones.

Table 6. Male upper forewing lunules covering parts of Europe.

No.	Locality	5&6mufl	0-4mufl	Total
1	Scotland *artaxerxes*	22	349	371
2	N England intermediates	120	412	532
3	C&S England *agestis*	661	137	798
4	Spain	80	58	138
5	Switzerland	11	105	116
6	Scandinavia	31	136	167
	Totals	925	1197	2122

A further statistical test follows in Table 8 to see if there is any similarity between the intermediates in the three countries, again using np± k√ (npq) with reference to the combined north of England figures in Table 6 where p = 120/532 = 0.2256. It can be seen that the intermediates from all three countries are statistically similar.

Table 7. Statistical check on British colonies.

No.	*Locality*	*Total*	5&6 mufl	5&6 mufl%	np	k√(npq)	*In/Out*
1	Scotland *artaxerxes*	371	22	5.93	161.72	18.72	Out
2	N England intermediates	532	120	22.56	231.90	22.42	Out
3	C&S England *agestis*	798	661	82.83	347.85	27.46	Out

A check on Scottish areas using 0 mufl where p = 187/371 = 0.504 follows in Table 9. Numbers 5, 7 and 8 are outside the 5% significance limits, indicating both some variation and a better penetration by intermediates from the south. The Swiss figures from Table 10 (p = 0.744) have a distinctly higher average than Scotland; therefore the possibility of a stable zone with a 0 mufl content of say 50-60% is unlikely.

Table 8. Statistical comparison of intermediates.

No.	*Locality*	*Total*	5&6 mufl	5&6 mufl%	np	k√(npq)	*In/Out*
1	N England intermediates	532	120	22.56	120.0	18.9	In
2	Spanish intermediates	40	10	25.0	9.02	5.18	In
3	Swiss intermediates	34	11	32.35	7.67	4.78	In

For Table 10, data from all Swiss *allous* specimens give p = 61/82 = 0.744. Results indicate that Swiss *allous* colonies are not all within the 5% significance limits: the variation is therefore due to variable penetration from "*agestis*".

Table 9: Statistical checks on Scottish *artaxerxes*.

No.	*Locality*	*Total*	0mufl	0mufl%	np	k√(npq)	*In/Out*
1	North of Inverness	13	10	76.9	6.55	3.53	In
2	Aberdeenshire, Banff	32	16	50.0	16.13	8.00	In
3	Inverness, Nairn, Moray	39	20	51.3	19.66	6.12	In
4	Kincardine, Angus	63	35	55.6	31.75	7.78	In
5	Perthshire	117	72	61.5	58.97	10.60	Out
6	Fifeshire	25	12	48.0	12.6	4.9	In
7	SE Scotland	47	15	31.9	23.69	6.72	Out
8	SW Scotland	35	7	20.0	17.64	5.80	Out
	Totals	371	187	50.4			

Table 10: Statistical checks on Swiss *allous*.

No.	*Locality*	*Total*	0mufl	0mufl%	np	k√(npq)	*In/Out*
1	Val Bever (GR)	12	12	100.0	8.93	2.96	Out
2	Haldenstein (GR)	19	17	89.5	14.14	3.73	In
3	La Luette (WA)	10	7	70.0	7.44	2.70	In
4	Airolo (TI)	13	6	46.2	9.67	3.08	Out
5	Kandertal (BE)	9	4	44.4	6.70	2.57	Out
6	Mitholz (BE)	8	6	75.0	5.95	2.42	In
	Totals	82	61	74.4			

Table 11: Statistical checks on Spanish *cramera*.

No.	*Locality*	*Total*	6mufl	6mufl%	np	k√(npq)	*In/Out*
1	Fuente Joco (Tenerife)	11	11	100.0	6.63	3.18	Out
2	Casa de Campo (Madrid)	36	22	61.1	21.71	5.75	In
	Totals	73	44	60.3			

In Table 11 covering Spain, since *cramera* is the best lunulated of all the *Aricia*, data have been restricted to 6 mufl. Colonies with 100% 6 mufl exist in Spain – records obtained simply do not have enough males from any one area to note them in the Table, but also there is no doubt that significant areas have lower lunulation due to variable penetration via *montensis*. In the Table, p = 44/73 = 0.603.

Discussion

At its western limit the genus *Aricia* stretches from the Canaries, latitude 28°N, through Morocco, the Iberian peninsula, France, Benelux, Britain and Denmark to north Norway at latitude 69.5°N. Therefore, Britain (excluding the Orkney and Shetland Islands) at 50-58°N, lies roughly in the middle. It so happens that it contains a significant proportion, though by no means all, of the variation encountered in *Aricia*. Any overview must take account of the fact that males in the Canaries all have 6 ufl, while males in Scandinavia north of 60°N have no records of either 5 or 6 ufl. As a result of the data from Spain and Switzerland, specimens from the mountain ranges in these countries are seen to be broadly similar to those north of 60°N. It is simplest to split the discussion into a consideration of the three countries, starting with Britain and further north, followed by Switzerland, Spain and the Canaries, with a subsequent general summary.

Britain and further north

The pertinent question, "does the approach of quantified upper forewing lunulation give an accurate indication of one aspect of the genetic make-up of *Aricia*?" has to be asked and an answer attempted. Favourable evidence is mounting – two major forecasts (Smyllie, 1992a, 1998), have been backed by genetic studies. Additionally, the comment that a colony in north Germany might prove to be similar to the one at Pickering in Britain (Smyllie, 1995) was verified at Inseln Rügen thanks to the interest and expertise of Dr Klaus Schurian (Smyllie, 1998).

The Brown Argus, *agestis*, extends from the south coast of England up to and including the Yorkshire Wolds in the east, latitude 50 to 54°N. It can be seen from Table 1 that *agestis* is statistically consistent as far as mufl is concerned. The variation which does occur has always been within the 5% statistical limits and, since no account has been taken of variation in foodplant, whether the specimens were first or second brood, and whether the British climate was good, bad or indifferent in the various years that samples were obtained, it has to be concluded that none of these, or indeed any other factors, have had an appreciable statistical effect. Specimens from continental Europe, admittedly in small numbers, have been taken from several different collections and their figure is also within the allowed variation. So also has the colony at Mainzer Sand near Frankfurt-am-Main in central Germany at Lat. 50°N.

White discal scales occur in British *agestis* in varying numbers: approximately one male in three and two females in three are affected on the south coast. The earlier comment (Asher et al., 2001) that genetic research has confirmed the relationship between Scottish *artaxerxes* and Scandinavian *allous* indicates that either can provide a northern element in *agestis*. An experiment carried out by Dr Schurian, not the only one carried out by various authors, linked the formation of white scales to a cool temperature early in the pupal stage (Smyllie, 1998). So, *artaxerxes* is centred on Scotland, and has a characteristic of white discal spots which allow a decreasing presence of white scales to be tracked down to the south coast of England (Smyllie, 1997). At the same time, the ocelli (black centres in the underwing spots) can hardly be seen in Scotland, but increase significantly as far away as the English south coast. Several "blue" butterflies have white rings round black centres in their underside spots and the origins of these are likely to be similar to *Aricia*. The white discal scales in *agestis* failed to make it beyond the English south coast prior to the Channel being formed. This is important, because it means that the formation of *artaxerxes* from *allous* is very likely to be an event which has occurred since the last ice-age. On mainland Europe there was no similar obstacle to the southward penetration of *allous*. While there is evidence of white discal scales in any English or Welsh *agestis* colony, including the very occasional white spot not only in southern England but also in southern Scandinavia (Higgins et al., 1970), there is no such presence in northern France. It is probable that there are minor variations in the composition of *agestis* without the overall lunulation stability being appreciably affected, and *agestis* is notable in that, once away from the extremities, it is the only *Aricia* which has consistent lunulation over considerable distances.

One interesting feature of *Aricia* in northern England is that significant changes in lunulation can occur over short distances. The male lunulation near

Pickering (OS grid square SE 88), at the point of change to "intermediates", is about half of that in the nearest Yorkshire Wolds *agestis* colony (grid square SE 86) only 15 km distant. The considerable variation in lunulation between north of England colonies can be seen in Table 2. The largest difference occurs between coastal and inland Durham colonies, which are only about 15 km apart at their nearest points. In North Wales, these distances may be much less. The status of the north of England colonies was investigated mathematically to find out if subspecies *salmacis* could occur, or if *artaxerxes* and *agestis* could co-exist at the same site, or neither of these – therefore pointing to hybrids (Smyllie, 1998). The first two were disproved, leaving hybrids. The possibility of these differences being due to random migration, or inclement weather killing a proportion of the population at a critical stage, or some other factor, remains to be clarified. This variability in north England, particularly in some adjacent colonies, coupled with the consistency in lunulation of *agestis*, and "phased emergence" (see later), must be borne in mind when considering any general theories concerning *Aricia*.

Turning now to Scotland and *artaxerxes*, the average lunulation is much lower than the north of England, and yet south-west Scotland (where most of the colonies are on or near the Solway Firth coastline – very little further north than the Durham coast) has better lunulation than any Durham coast colony. The variation in lunulation continues through Scotland, but with an average of 5.9% males having 5&6ufl compared with the north of England's 22.56%, it is simplest to view the situation as a combination of reducing lunulation and related variation as one goes further north. This effect is mirrored in Denmark, southern Norway and Sweden where the latitudes are similar to northern England and Scotland. North of latitude 60°N, the position appears to have settled down with no 5&6ufl occurring in 36 males from Norway and Sweden. In the most northerly colony in north Norway, near Lyngenfjord, no males were seen with any upper forewing lunules although hind-wing lunules were present (Høegh-Guldberg, 1966). In this respect the situation is similar to the higher altitudes in Spain and Switzerland.

Spain

Table 4 gives details of very poorly lunulated *morronensis* which, as the only Spanish *Aricia* with this lunulation (no males with 5&6 ufl in 25 and only one with 2-4 ufl), must be the equivalent of *allous* in Switzerland, even though there are morphological differences between the two races. Because of the poor mufl, upper hindwing lunules in males were also recorded for both Spain and Switzerland. Most specimens had three, four or five hindwing lunules but there were some from both countries without any lunules on the upper wings (var. *unicolor*):

Spain – 3 out of 25 males (12%) and 1 out of 17 females
Switzerland – 13 out of 82 males (15.8%) and one out of 11 females

From the twenty-five males seen, Spanish *morronensis* has less penetration by *cramera* when compared with the parallel situation in Switzerland, but most males still have significant lunulation on the hind-wings. More checks would be needed to see if there was greater variation in some of the mountain regions.

The statistical exercise in Table 8 has showed that *montensis* is similar to the north of England "intermediates" and Swiss "*agestis*". No examples of *agestis* were seen, but Spain is a big country and in view of its stability in England it will be surprising if *agestis* does not occur where the change from *cramera* to *montensis* takes place over relatively large distances.

In the Canaries and at several, though not all, Spanish localities, *cramera* males can have 100% with 6 ufl. However, even at Fuente Joco (Canaries) the relative sizes of lunules in individual males vary. At Casa de Campo, near Madrid, not all males have 6 ufl: 34 out of 36 have 5&6 ufl, and only 22 have 6 ufl. These aspects point to a variable 0 lunule component and this must have come from *morronensis* via *montensis* and, where appropriate, *agestis*. There is doubt about the ability of *cramera* to cross-breed nowadays, but the situation is not clear-cut and one conclusion is that *cramera* is "*in statu nascendi*" – it has not yet achieved full species status (Schurian, 1995). This statement can be extended to all other *Aricia* races. All the evidence points to interpenetration between lunulation extremes and this will hinder any drive to distinct species. Another aspect of *cramera* is that var. *luxurians* is found widely in colonies distinctly north of Spain. One incident out of many is recorded for a female on the Durham coast with lunules that would make an *agestis* female envious (Jarvis, 1969). It is usually females which are stated to be "overlunulated".

It could be that development towards separate species is faster in Spain, or it may be that more data from different mountain regions will throw up more variation. The former possibility would account for the more obvious differences in morphology exhibited by *morronensis*.

Switzerland

Swiss *allous* localities range from 600-1900m above sea level and one of the least well lunulated is at Haldenstein at only 600m, the lowest altitude recorded. Moreover, this is quite near the Schannfig area where Bischof has noted bivoltine emergence with the probability of the colonies there being at least in part "intermediate". This is one example of variation in lunulation similar to Britain. Examination of Table 5 shows that there is wide variation in the 0 mufl content (44.4-100%). A statistical check in Table 10 similar to that carried out in Table 1, but using 0 mufl, shows that three out of the six mentioned are outside the 5% significance zone, Nº 1 high, and Nºs 4 & 5 low. This indicates that there is variable penetration into *allous* via Swiss "*agestis*". The situation is roughly similar to Scotland although the sequence regarding increasing penetration at the 0 mufl end is Spain, Switzerland, Scotland.

Regarding "*agestis*", it has already been stated that the colonies here are in the intermediate category. Although the data for *agestis* comes largely from Britain, there is backup from limited European examples together with the statistical consistency. Moreover, the Swiss data fit in statistically with the north of England colonies. Following the pattern in England it is suggested that the Swiss intermediates contain *allous* and *agestis*. It would appear that *agestis* does not occur in Switzerland.

Phased Emergence

This refers to a field observation that better lunulated *Aricia* male butterflies emerge first, to be followed through the flight period by less well lunulated specimens. Because females are better lunulated than males, the effect is less noticeable, particularly in *agestis* colonies. I became aware of the phenomenon by chance: a visit on 20 May 1989 to Watlington Hill in Oxfordshire to note the early stages of *agestis* there ended with my leaving my cameras behind. Luckily they were picked up by the police. I collected them nine days later, and revisited the site. On my earlier visit all eleven males seen had either 5 or 6 ufl. Out of nine males, seven has 5 or 6 ufl, one had 4 ufl and the other had 3 ufl (Plate M). This was not proof, but merited further investigation since I felt that I should have seen any 3 or 4 mufl specimens during the previous quite lengthy visit. During 1992, I visited Coombs Dale south of Sheffield in the Peak District, at weekly intervals, carrying out a type of transect walk to fit in with the terrain and objective of counting lunules (Smyllie, 1992b). Between 31 May and 13 June (the first three visits), only 6 mufl were seen. On 21 June, 5 mufl specimens appeared with 4 mufl following on 28th. The only example of 3 mufl appeared on 5 July. The decrease is not entirely smooth and having become aware of the phenomenon it was possible to pick up literature references. First, the occurrence of a univoltine portion in bivoltine *agestis* at Royston, Hertfordshire (Jarvis, 1969); secondly details of specimens from Sandhammaren, southern Sweden, showing the decrease in mufl (again not entirely smooth) during the first brood, rising abruptly at the start of the second (Høegh-Guldberg, 1966). This is an intermediate colony (Smyllie, 1995), so a significant portion will be single-brooded, although the climate is good enough for a distinct partial second brood.

The phenomenon has been described in some detail because it is considered important. If well lunulated and poorly lunulated races were to coincide and hybridise, what would happen as far as their normal expectation of bivoltine and univoltine emergence is concerned? At present the climate in northern England is, normally, not good enough for bivoltine emergence, but it is in southern Sweden. Here, *agestis*-rich butterflies will be bivoltine, *artaxerxes*-rich will be univoltine, and, somewhere in between, diapause will take place at a variable point depending on the weather actually experienced and the precise constitution, presumably genetic, of the larva. Diapause will control the point from where development takes place the following spring, and even then the *agestis*-rich portion will continue to develop more quickly. So one characteristic of *Aricia* colonies will be that their flight periods will be more spread out than other butterflies with a less complex history. Another aspect is that species with similarly extended flight periods are likely to have a similar degree of complexity. Yet another point to be noted is that in these days of increasingly sophisticated equipment and techniques it will still be possible to pick up important information from straightforward field observation. Phased emergence supports the hypothesis that *Aricia* intermediates are hybrids between the well and poorly lunulated races on either side. This is particularly relevant for example in Spain where present morphological differences between *cramera* and *morronensis* may cast doubt on either *agestis* or *montensis* having arisen from the first two. The missing link is that we do not know what the situation was when this event is thought to have happened. DNA analysis should be able to clear up the situation.

Eggs

T. Lloyd Newman considered that the earliest stages of a butterfly were more likely than the adult insect to give an indication of its origins (Acworth, 1947). Scanning electron microscope photographs of four eggs are shown (Plate N, Figs. 1-4). The pictures indicate some differences. For example, the Perthshire egg (Fig. 1) has higher reticulation than that from Kettlewell (Fig. 2), which is higher than the others. In all the eggs, however, the areas bounded by the white ribbing vary both in size and shape. If their origins were to have been quite different there would surely have been much greater differences in the features mentioned. Thus, although it is very likely that individual eggs from the same site will differ, it nevertheless seems reasonable to postulate that they have come from a common ancestor.

Genetic analysis and quantified lunulation

Assuming that there is further correlation between quantified lunulation data and DNA analysis, it would seem prudent, as far as parts of Europe are concerned, to gather information via museums as a first step and subsequently concentrate on areas of particular interest via DNA analysis. This should help to save time and expense on what so far has been a relatively slow process. Provided the specimens are available it is much easier to build up considerable numbers for any area via collections and this is a positive aid in providing extra focus through statistical analysis.

Summary

The information provided by quantified upper forewing lunulation has indicated parallels between races in Britain, Spain and Switzerland for the *Aricia* genus. Spain has the most complete range, with Britain and

Switzerland having parts. The evidence indicates very poor and very good lunulation at the extremities with some penetration by the other fraction everywhere, and a relatively unstable intermediate zone in-between. As lunulation increases from the poor end there is no positive indication of a stable zone. Towards the very good end *agestis* does form a stable zone. The following hypotheses are made regarding the history of *Aricia* with the comment that the data will not change whether the hypotheses are eventually agreed to be correct or otherwise:

- The genus *Aricia* arose from a common ancestor (general similarity of eggs from different British regions).

- Gradually two races developed, one which was well lunulated – lower altitudes and further south; the other which was poorly lunulated – higher altitudes and/or further north.

- They did not intermingle before having progressed to 0 lunules and 12 lunules respectively on the upper wings (if this was not the case, where did var. *unicolor*, with no upper wing lunulation, and var. *luxurian*s, with 12 full upper wing lunules – particularly in females - come from?).

- This did not happen overnight – suggested time-scale tens of thousands of years. This postulates very small year-by-year increments in lunulation and ground colour pigmentation, either up or down, depending on the climate experienced. It is interesting to speculate on the possibility of "*Aricia* dendrology" being available at some future date either via genetic or morphological checks. Some event or events subsequently caused these races to overlap: the suggested cause is the last ice-age, followed by a climatic optimum which started at the end of the Younger Dryas event about 11,500 years ago and then lasted for over 2000 years, when the temperature was on average higher than it is now (Lamb & Sington, 1998). Since this event, the picture presented via lunulation has not been significantly blurred. In spite of any morphological differences and possible mating difficulties today, the races could still have coincided and subsequently crossbred about 10,000 years ago.

- Recent global warming has allowed northwards expansion of 15 British species including *agestis* (Fox, 2001). The Brown Argus has been tracked through Lincolnshire and into Yorkshire in the last 10 years or so, reaching West Yorkshire in 2000, a distance of over 100 kilometres. So far there has not been any detectable movement from the univoltine *agestis* colonies or from the north of England intermediates. So there is relative movement between *agestis* and other colonies. Given continuing warmth, within a few years the migrants will impinge on the static colonies and provide a parallel to what has happened previously.

- The main overlap area may well have been relatively restricted initially. It could then have been followed by 'gene flow' where wanderers from the original overlap colonies coincide over long periods of time with nearby colonies, and gradually spread lunulation (or the lack of it), over considerable distances so that eventually there is some interpenetration everywhere.

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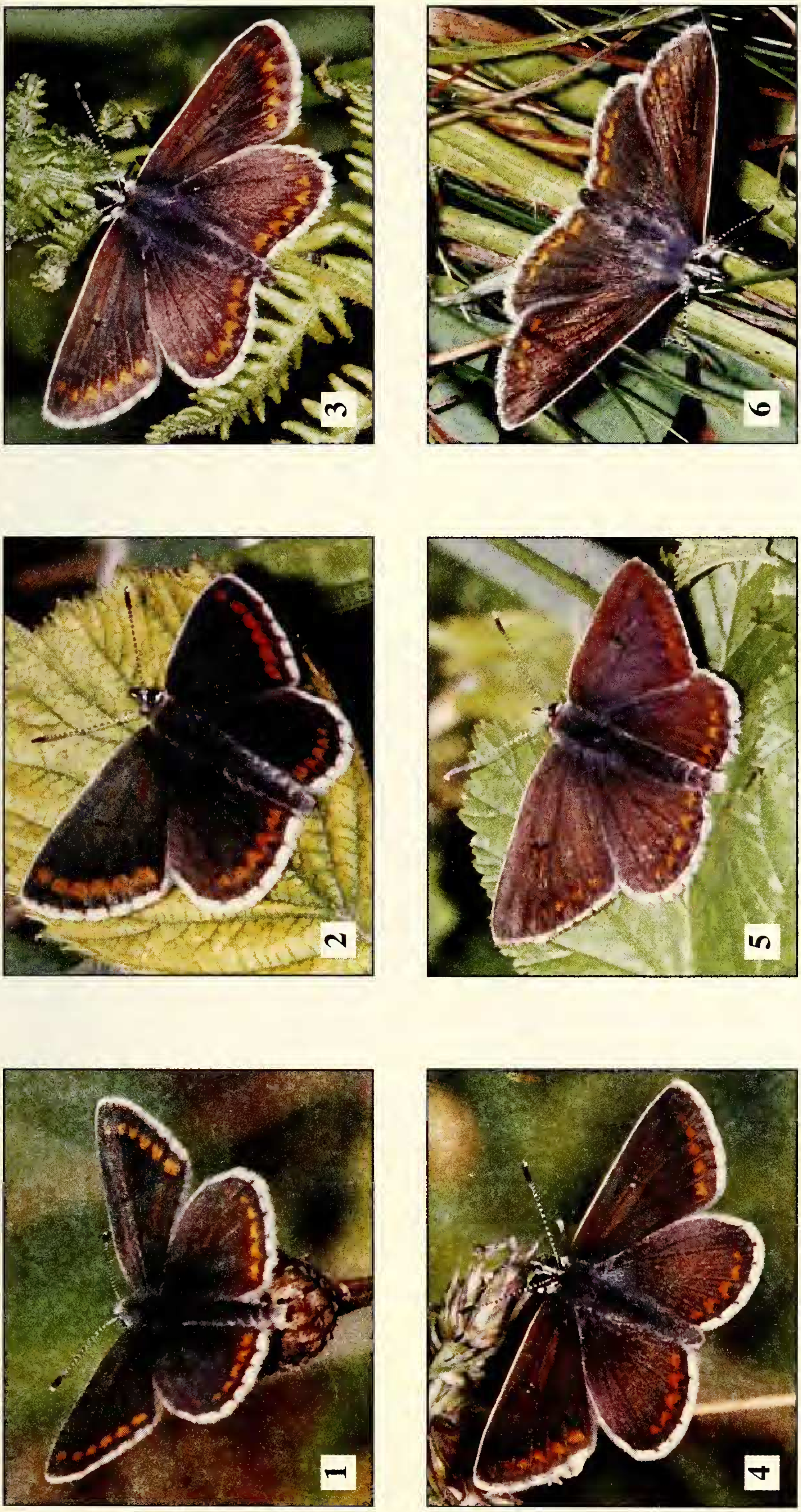

Plate M. Brown Argus *Aricia agestis* at Coombs Dale, Peak District 1992.

1. ♂ 31.5.92, 6 ufl 2. ♀ 6.6.92, 6 large ufl 3. ♂ 21.6.92, 6ufl 4. ♂ 21.6.92, 5 ufl 5. ♂ 5.7.92, 4 ufl 6. ♂ 5.7.92, 3 ufl

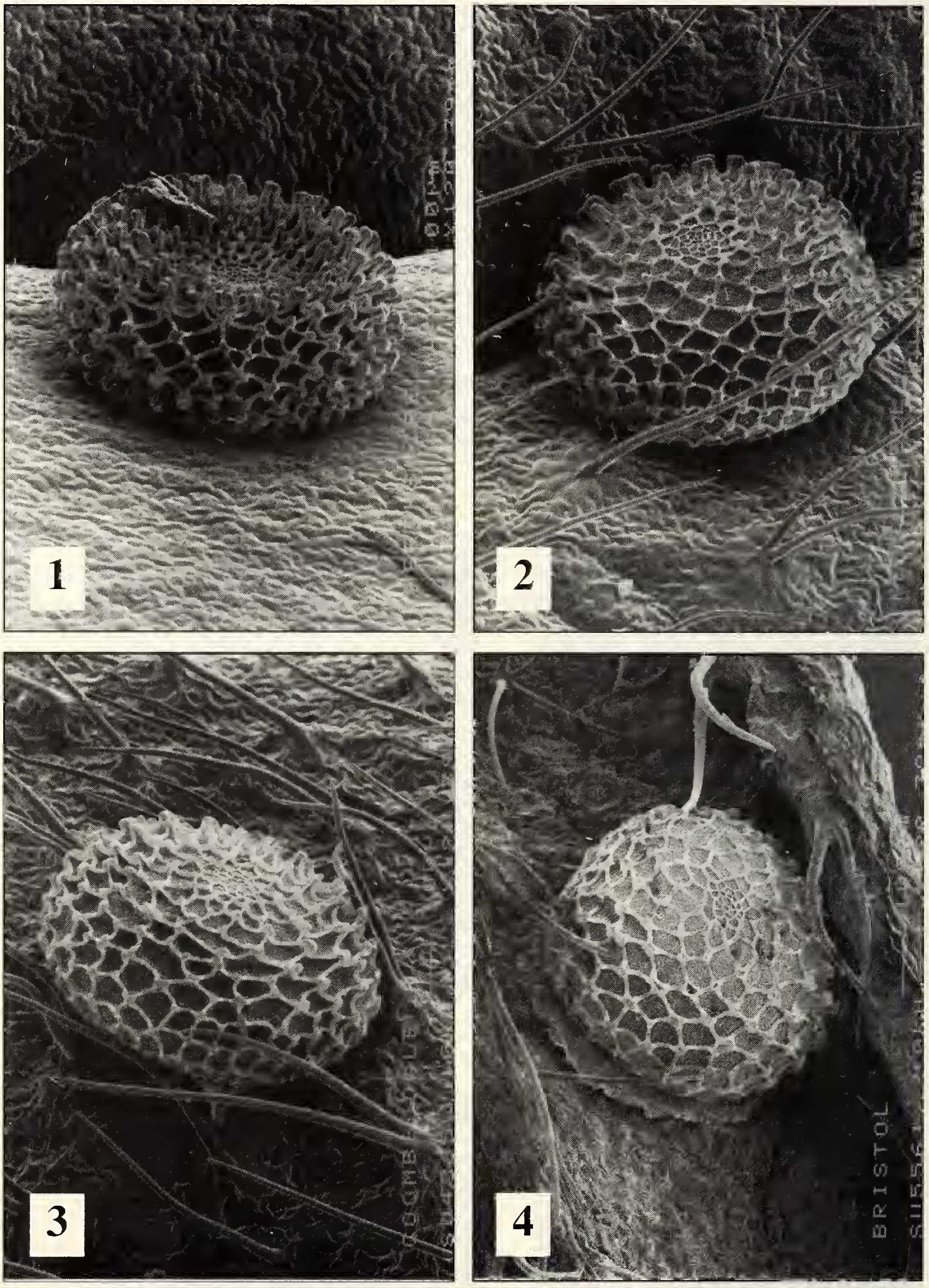

Plate N: Scanning electron micrographs of *Aricia* eggs.

1 Perthshire – *artaxerxes*

2 Kettlewell, north Yorkshire – intermediate

3 Coombs Dale, Peak district– univoltine *agestis*

4 Portishead, Somerset – bivoltine *agestis*